Fruit-Based Tolerance to Damage by Beet Armyworm (Lepidoptera: Noctuidae) in Tomato

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ABSTRACT Damage to fruit of eight accessions and cultivated varieties of tomato by natural infestations of beet armyworm, *Spodoptera exigua* (Hübner), in Southern California ranged from 0.1 to 10%. This field damage was significantly correlated with 9-d weight and survival of *S. exigua* larvae reared to pupation from third instar in the laboratory on fruit of these tomato test entries. Two accessions of *Lycopersicon esculentum* variety *cerasiforme* and one small-fruited cultivated variety of *L. esculentum* sustained lowest damage in the field (1–50% of susceptible controls). *S. exigua* larvae had reduced survival and reduced 9-d weight (≈20% of susceptible controls). Time to pupation was also increased on these three lines (30% greater than controls). The resistant fruits had high concentrations of total glycoalkaloids in the fruit tissue (5.4 to 25.4 mg/g dry weight versus 1.8 mg/g in a susceptible fruit) and this may have been the basis of the antibiosis. Phytosterol concentrations in the fruits were not sufficiently high to potentially alleviate glycoalkaloid toxicity. In binary choice tests between fruit and foliage of the most resistant line, *L. esculentum* variety *cerasiforme* LA 1320, larvae of *S. exigua* fed on fruit 70% less than larvae in choice tests between the fruit and foliage of susceptible 'VFN 7718'. Larval nonpreference for fruit apparently contributes to resistance in LA 1320. The resistance to *S. exigua*, of LA 1320 predicted by this mechanism, is close to observed levels of resistance in the field.

KEY WORDS host-plant resistance, tolerance, antibiosis

AS PART OF an effort to develop sustainable pest management of insect pests of fresh-market tomato, we have been investigating host-plant resistance to the key pests of this crop in Southern California and Mexico. A major target has been the beet armyworm, *Spodoptera exigua* (Hübner), which has become one of the most serious pests of tomato in this geographic area (Lange & Bronson 1981, Brewer et al. 1990).

Several accessions of *Lycopersicon esculentum* ssp. *cerasiforme* (Dun.) variety A. Gray (*cer*) and *L. pimpinellifolium* (Jusl.) Mill. (*pim*) are resistant to damage by natural populations of *S. exigua* (Eigenbrode et al. 1993). Resistance to *S. exigua* in *cer* and *pim* may not be as strong as in *Lycopersicon hirsutum* (f. *typicum* Humb. & Bonpl. or f. *glabratum* Mull.) (Farrar & Kennedy 1992), but because *cer* and *pim* are more closely related to cultivated tomato than *L. hirsutum* (Rick 1978), incorporation of this resistance into cultivated tomatoes may be easier. The potential benefits of even partial resistance in integrated pest management, justify additional investigations of insect resistance in *cer* and *pim*.

Resistance to *S. exigua* in *cer* and *pim* appears to depend more on characteristics of the fruit than on characteristics of the foliage. Growth and survival of *S. exigua* are much lower on the fruit of *cer* LA 1320, *pim* LA 1606 (Eigenbrode et al. 1993), *cer* LA 1310, and *pim* LA 1335 (Juvik & Stevens 1982), than on the fruit of standard *esc* varieties. *S. exigua* survival is also very low on the fruit of cherry-type cultivar 'Tiny Tim' (Eigenbrode et al. 1993), which has *pim* in its pedigree (Graham 1959). In contrast, foliar antibiosis to *S. exigua* is lacking in LA 1320, LA 1335, and 'Tiny Tim' (Eigenbrode et al. 1993).

The current study was designed to understand better the mechanisms of fruit-based resistance to *S. exigua* in *esc* and *cer*. The experiments determined the relationship between fruit antibiosis and susceptibility to damage in the field among eight genotypes, examined the role of cuticle toughness and alkaloid content in producing fruit antibiosis, and measured the relative preference of *S. exigua* for fruit and foliage of the most resistant *cer* accession, LA 1320, as compared with a susceptible variety.

Materials and Methods

The study included six *esc* and two *cer* accessions. The *cer* accessions were LA 1320 and LA 1310. *Esc* types were 'VFN 7718' (Petoseed), a susceptible fresh-market variety; 'Yellow Pear'

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and 'Tiny Tim', two older cultivated varieties reported to have low susceptibility to *H. zea* (Fery & Cuthbert 1974) or *S. exigua* (Eigenbrode et al. 1993); NSL 27243, which has a thickened pericarp; LA 986, which has several monogenic mutations (s, compound inflorescence; bk, beaked; Wo^m, Morgan's wooly; o, orange; aw, no anthocyanin; p, peach; d, dwarf) but most importantly, appears to have a very thin fruit cuticle; and LA 533, which has the same genetic background as LA 986 but does not have the mutations and has a more standard cuticle. NSL 27243 and LA 986 were included in these experiments because their pericarp or cuticle characteristics were considered likely to influence susceptibility.

Seedlings of the test entries were transplanted in the field in mid-May 1992 at the University of California at Riverside. The plants were arranged in a randomized complete block design with three replicate single-row plots of seven plants per test line. Plants were spaced 40 cm within the row and 2 m between rows, and they were drip irrigated. The soil was an Arlington loam, pretreated with 16:20:0 N:P:K at 450 kg/ha.

Blossoms on test plants were tagged at anthesis. Fruit were harvested at 4 wk after anthesis for bioassay and chemical and physical analysis. Beet armyworm were reared in groups of 10 in 0.5-liter paper cans containing one to three fruit of the test line, as described by Eigenbrode et al. (1993). Larvae were introduced at third instar, the earliest instar capable of successfully feeding on susceptible fruit (unpublished data). Fruit and paper-towel linings of the cans were replaced every other day. Pedicel scars of the fruit were filled with paraffin to prevent larvae from entering at this vulnerable point, which is inaccessible when fruit are on the vine. Larval weight at day 9, survival to pupation and to adult, and days to pupation were recorded.

For the first 10 d of the test, each time fruit was replaced in the bioassay, the cuticle toughness of a subsample of four fruit from each line was measured. The measurements were made with a UCR fruit firmness penetrometer (Coggins et al. 1965), which measures the force required to puncture the fruit cuticle with a 1-mm drill blank. A total of 20 fruit were measured for each line and each measurement consisted of the average of four penetrations per fruit.

A second field experiment was planted on 7 July at the University of California South Coast Research and Education Center in Santa Ana. Cultural practices and design were the same as those used in Riverside except the soil was a Sorranto loam, fertilized preplanting with 15:20:0 N:P:K at 55 kgN/ha. The plants were infested naturally by *S. exigua*, which occurs in the late summer in coastal southern California. On 30 September, damage to fruit caused by *S. exigua* was recorded on 100 fruit from each of the three replicate plots for each test line except LA 986, which did not set sufficient fruit. Data were converted to a percentage of fruit damaged.

After damage assessments were made on the South Coast experiment, undamaged fruit of LA 1320, LA 1310, 'VFN 7718', and 'Tiny Tim', 4 wk after anthesis, were used in a second laboratory bioassay. The bioassay was as described above, but the fruit were either intact or ≈ 2 cm^2 of their cuticles were removed to permit larvae access to underlying pericarp tissue. Each line by treatment was replicated 10 times, and a replicate consisted of 10 larvae in a 0.5-liter paper can. Fruit were replaced every 24 h and survival of larvae was determined after 120 h.

Total glycoalkaloid (TGA) content was also determined for the fruit of 'Tiny Tim', 'VFN 7718', LA 1310, and LA 1320 used in this bioassay. Eight 100-g samples of fruit were taken during the bioassay, held at −60°C and subsequently lyophilized. TGA analysis was modified from Fitzpatrick & Osman (1974). Powdered, lyophilized fruit tissue ($\approx$0.2g) was extracted for 15 min with agitation in 25 ml of 80°C 5% acetic acid. The extract was filtered and the flask and filter paper was washed with 5 ml of hot acetic acid. The filtered extract was brought to pH 10 with ammonium hydroxide ($\approx$5 ml) and held on ice for 2 h. Precipitates were removed by centrifugation at 31,000 *g* for 30 min at 0–4°C. The pellet was washed twice in distilled H_2O, recentrifuged, and the supranatent was removed by pipette. The washed pellet was then dried in a lyophilizer, dissolved in 10 ml of absolute methanol, and titrated with 10^{-3} M bromphenol blue in a 10% solution of phenol in methanol. The method determines total glycoalkaloids, which in tomato fruit is 100% α-tomatine (Roddick 1974). TGA values for each sample were based on an average of three determinations.

Since it has been demonstrated that the toxicity of α-tomatine to *S. exigua* in artificial diets or in plant extracts can be alleviated by phytosterols (Bloem et al. 1989), we also determined the total amounts of these compounds in subsamples of the powdered fruit tissue used for the TGA analysis. Extraction and analysis of phytosterols and phytosterol esters was modified from Indyk (1992). Recovery of known sterols using this extraction method was $\approx$98%. Analysis was by high-pressure liquid chromatography (HPLC) and quantification was by external standards of cholesterol, β-sitosterol, campesterol, stigmasterol, and desmosterol (Sigma, St. Louis MO). The identity of these five phytosterols was confirmed by coupled gas chromatography/mass spectrometry of fractions collected from the HPLC. Three unidentified phytosterols comprised 22% of the sterol fraction, based on flame ion detector peak areas on the gas chromatograph. Concentration of these three sterols was

Table 1. Performance of *S. exigua* larvae on fruit (4 wk after anthesis) of eight tomato genotypes, cuticular toughness of test fruit, and field damage by *S. exigua* to these genotypes

Test line	Survival to pupation, %[a]	Survival to adult, %[b]	9-d Wt, mg[c]	Days to pupation[d]	Cuticle toughness, g/mm^{2}[e]	*S. exigua* damage, % of fruit[f]
LA 1310	11.0 ± 4.8c	1.0 ± 1.0d	39.2 ± 4.6d	15.7 ± 1.9bc	336 ± 7c	0.5 ± 0.5d
LA 1320	11.0 ± 3.5c	6.0 ± 2.7de	29.6 ± 0.3d	22.1 ± 1.0a	392 ± 10b	0.1 ± 0.1d
NSL 27243	42.0 ± 7.0ab	36.6 ± 5.0ab	95.4 ± 10.5bc	14.0 ± 0.3de	403 ± 15b	4.9 ± 1.2b
LA 533	54.0 ± 6.2a	47.0 ± 5.2a	113.7 ± 11.1b	14.3 ± 0.3de	409 ± 8b	4.0 ± 0.5bc
'VFN 7718'	47.0 ± 6.2a	27.0 ± 6.7bc	179.3 ± 38.8a	13.0 ± 0.2e	346 ± 5c	10.0 ± 0.6a
LA 986	44.0 ± 6.5ab	31.0 ± 4.6ab	105.4 ± 1.2bc	14.3 ± 0.4cde	254 ± 11d	—
'Tiny Tim'	10.0 ± 4.0c	10.0 ± 3.6d	42.4 ± 3.9d	16.8 ± 0.8b	439 ± 11a	5.3 ± 1.0b
'Yellow Pear'	29.0 ± 6.2b	15.0 ± 4.0cd	60.0 ± 1.3cd	14.8 ± 0.5cd	349 ± 6c	1.8 ± 0.7c

Mean separation with least significant difference; —, insufficient fruit set to assess damage. Means in each column followed by the same letter are not significantly different at 0.05 level.

[a] $F = 10.15$; df 7, 72; $P = 0.0001$.
[b] $F = 15.43$; df 7, 71; $P = 0.0001$.
[c] $F = 8.76$; df 7, 68; $P = 0.0001$.
[d] $F = 24.87$; df 7, 236; $P = 0.0001$.
[e] $F = 35.18$; df 7, 214; $P = 0.0001$.
[f] $F = 20.56$; df 6, 13; $P = 0.0001$.

estimated assuming their absorption at 212 nm was equal to that of cholesterol.

Preference of fourth-instar larvae for fruit versus foliage in LA 1320 and 'VFN 7718' was examined with a binary choice test between these two tissues, within each genotype. Larvae were placed in a 15-cm plastic petri dish with sections of fruit 4 wk after anthesis and with leaflets from the fifth node from the terminus from the same genotype. Because the fruit of the two test lines is very different in size (12 g, 2.5-cm diameter for LA 1320; 160 g 7.5–10-cm diameter for 'VFN 7718'), care was required to present sections of similar size in these tests. Fruit of LA 1320 was halved, and shallow sections of the fruit of 'VFN 7718' were cut with surface areas similar to halves of fruit of LA 1320. Four fruit sections were distributed around the edge of the petri dish with the cut surface down. The dish was then filled to a depth of 0.5 cm with molten paraffin, which solidified to form a seal around the cut surfaces of the fruit so only the undamaged fruit surface was exposed in the bioassay arena. Four leaflets were distributed around the edge of the dish, alternating with the embedded fruit sections. Five larvae were placed in the center of the dish. The location of the larvae was recorded at 3, 6, and 24 h after the beginning of the test. At 24 h, the number of fruit sections damaged, and the volume of leaf tissue and fruit tissue consumed, were recorded. Volume of leaf tissue consumed was determined by measuring leaf area before and after the test with a leaf area meter (Li-Cor, Lincoln, NE) and multiplying the difference of these values by the average thickness of the leaves (0.1 mm). Volume of fruit tissue removed was determined by injecting molten paraffin into the feeding wounds. The fruit was then frozen and thawed and the paraffin castings of feeding damage were washed clean of fruit residues. The volume of these castings was then determined by displacement of ethanol in a graduated cylinder. The experiment included 12 replicates for each genotype.

Differences in survival and growth in both assays were analyzed with analysis of variance (ANOVA) and means were separated with Fisher's protected least significance different test (LSD). Comparisons in the choice test were made with Student's *t*-test. Correlations were Pearson coefficients. Proportional data were angularly transformed to stabilize variances. All analyses were performed using SAS (SAS Institute 1992) procedures GLM, CORR, TTEST, and MEANS.

Results

Survival and growth (9-d weight and days to pupation) differed significantly among *S. exigua* larvae reared on fruit of the eight test entries (Table 1). The fruit of LA 1320, LA 1310, and 'Tiny Tim' were the least suitable for larval survival and growth. The fruit of susceptible control 'VFN 7718' and NSL 27243, LA 986, and LA 533 were the most suitable and did not differ from one another. The fruit of 'Yellow Pear' was intermediate between the resistant and susceptible test entries.

Damage from *S. exigua* in the field was correlated with 9-d larval weights on fruit over all the test lines ($r = 0.85$, $n = 7$, $P < 0.01$). 'Tiny Tim' was the outlier in this relationship (Fig. 1) and without this line $r = 0.980$, $P = 0.005$. Damage was not correlated significantly with survival to pupation on the fruit of the test lines ($r = 0.59$, $n = 7$, $P = 0.1$). Intermediate damage to 'Tiny Tim' also had a strong effect on this relationship and without this line $r = 0.771$, $n = 6$, $P = 0.05$. Correlations between days to pupation or survival to adult and damage were not significant with or without 'Tiny Tim'. Survival on the four

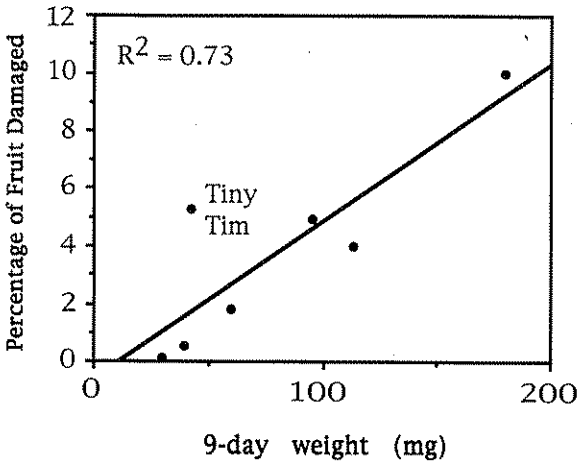

Fig. 1. Regression of 9-d survival of larvae on fruit on the percentage of fruit damaged in the field among seven tomato genotypes.

lines in the 120-h bioassay also was correlated to damage to these lines in the field ($r = 0.96$, $P = 0.01$).

Larval performance was not related to cuticle toughness (correlation coefficients: versus survival to pupation, −0.32; versus survival to adult, −0.08; versus 9-d weight, −0.28; versus days to pupation, 0.36; all values not significant at $P = 0.05$). The line with the thinnest cuticle, LA 986, was not better for larval development than thicker-skinned LA 533 or 'VFN 7718'. Cuticle toughness also was not related clearly to survival in the 120-h bioassay (Table 2). Providing larvae access to underlying pericarp tissue by peeling the cuticle significantly increased *S. exigua* survival across all four genotypes ($F = 6.10$; df = 1, 3; $P = 0.0159$), but there was not a significant interaction for survival between the cuticle peeling treatment and genotype based on analysis of variance ($P > 0.5$).

Table 3. Choice test with fourth-instar *S. exigua* between foliage and fruit of resistant LA 1320 and susceptible 'VFN 7718'

	'VFN 7718'		LA 1320
Vol foliage removed, cm^3	0.61 ± 0.11	NS	0.38 ± 0.09
Proportion of leaflets damaged	0.70 ± 0.14	NS	0.63 ± 0.06
Vol fruit removed, cm^3	0.56 ± 0.11	***	0.09 ± 0.04
Proportion of fruit damaged	0.45 ± 0.06	***	0.13 ± 0.05
Fruit vol:foliage vol removed	0.50 ± 0.06	*	0.20 ± 0.08
Proportion of larvae located on fruit			
Time, h			
3	0.21 ± 0.05	**	0.03 ± 0.02
6	0.27 ± 0.07	**	0.05 ± 0.03
24	0.33 ± 0.06	NS	0.20 ± 0.08

*, **, ***, significantly different at $\alpha = 0.05$, 0.01 and 0.001 Student's *t*-test.

TGA content of fruit of LA 1320 and LA 1310 was much greater than that of the cultivated varieties 'VFN 7718' and 'Tiny Tim' (Table 2). Total phytosterol content for the fruit of these four test lines was not as different as TGA content, although it was lower in 'VFN 7718' than in the other three test entries. The estimated phytosterol:tomatine molar ratio was <1 for fruit of all four lines (Table 2), indicating that phytosterols could not have alleviated potential toxicity of α-tomatine. LA 1310 and LA 1320 had 10 times as much α-tomatine as phytosterols on a molar basis.

In the choice test, a greater proportion of fourth-instar *S. exigua* was located on fruit versus foliage of 'VFN 7718' than on the fruit versus the foliage of LA 1320 at 3 and 6 h (Table 3). The proportion of fruit sections damaged, the volume of fruit tissue consumed, and the fruit proportion

Table 2. Survival of *S. exigua* on fruit (4 wk after anthesis) of four tomato genotypes with and without some cuticle removed to permit larvae access to pericarp, cuticle toughness, total glycoalkaloid content (TGA), total phytosterols, and water content of fruit

Test line	Treatment	5-d Survival, %[a]	Cuticle toughness, g/mm^{2b}	TGA, mg/g dry wt[c]	Total phytosterols, mg/g dry wt[d]	Phytosterol:tomatine[e]	H_2O, % of fresh wt[f]
LA 1310	whole	28 ± 8bc	363 ± 7c	26.3 ± 2.0a	1.01 ± 0.15a	0.11	91.4 ± 0.3b
	peeled	61 ± 10ab					
LA 1320	whole	19 ± 7c	388 ± 7a	22.3 ± 2.6a	0.86 ± 0.10a	0.11	91.1 ± 0.3b
	peeled	50 ± 9abc					
'VFN 7718'	whole	57 ± 10ab	315 ± 11b	1.8 ± 0.3b	0.49 ± 0.051b	0.76	93.5 ± 0.1a
	peeled	67 ± 10a					
'Tiny Tim'	whole	40 ± 11abc	395 ± 8a	5.4 ± 1.44b	0.88 ± 0.08a	0.44	93.0 ± 0.3a
	peeled	48 ± 10abc					

Mean separation with least significant difference; means in each column followed by the same letter are not significantly different at 0.05 level.

[a] $F = 2.28$; df = 7, 72; $P = 0.037$.

[b] $F = 15.53$; df = 3, 70; $P = 0.0001$.

[c] $F = 62.23$; df = 3, 27; $P = 0.0001$.

[d] $F = 4.50$; df = 3, 25; $P = 0.0117$.

[e] On a molar basis. The molar content of phytosterols and tomatine was estimated, assuming TGA to be 100% tomatine and using an approximate formula weight of 414 amu for the unidentified phytosterols (22% of gas chromatographic peak areas).

[f] $F = 34.29$; df = 3, 25; $P = 0.0001$.

of the total tissue consumed (volume of fruit consumed/volume of fruit + foliage consumed) after 24 h was greater for 'VFN 7718' than for LA 1320. The volume of foliage consumed in 24 h by the larvae did not differ significantly between 'VFN 7718' and LA 1320.

Discussion

The correlations between *S. exigua* growth and survival on fruit and the percentage of fruit damaged suggest that fruit characteristics can influence economic susceptibility to this insect in tomatoes. Fruit characteristics may be the only basis of resistance in some cases. The foliage of several less susceptible *esc, cer,* and *pim* accessions, including LA 1320 and 'Tiny Tim', is not substantially antibiotic to Lepidoptera (Sinha & McLaren 1989, Eigenbrode et al. 1993) and these accessions appear to support populations of *S. exigua* similar to those on susceptible varieties under natural infestations in the field (Eigenbrode et al. 1993).

Because fruit is rendered unmarketable by even small amounts of feeding, it would appear that fruit antibiosis alone would be unable to condition resistance. Antibiosis would have to be accompanied by larval nonpreference for less suitable fruit. Our data show that this is the case for LA 1320. The reduced larval preference for fruit of LA 1320, in combination with several other factors influencing damage can largely account for the low damage sustained by this accession. On a weight basis, LA 1320 has a smaller ratio of fruit to foliage (0.8) than 'VFN 7718' (2.6) (Eigenbrode et al. 1993). On a surface area basis fruit to foliage ratios are 0.023 for LA 1320 and 0.036 for 'VFN 7718' (unpublished data). Assuming larvae move randomly through the plant, and that the availability of fruit is proportional to surface area, larvae are about 40% less likely to encounter fruit on LA 1320 than on 'VFN 7718'. The number of fruit per 100 g of foliage is 3.0 for 'VFN 7718' and 16.2 for LA 1320 (recalculated from data of Eigenbrode et al. 1993). Therefore, a single feeding event will cause ≈0.2 times as much economic injury (percentage of fruit damaged) on the smaller-fruited genotype. Combining the estimates of the relative preference for feeding on fruit, the relative probability of encountering fruit and the effect of feeding on percentage of fruit damaged, LA 1320 is predicted to sustain $0.30 \times 0.60 \times 0.20 = 0.036$ as much damage as 'VFN 7718' under similar infestations.

Observed differences in damage between LA 1320 and 'VFN 7718' are only slightly higher than predicted. Average *S. exigua* damage to 'VFN 7718' over three growing seasons (1990–1992) at Santa Ana is 8.50% (Eigenbrode et al. 1993 and Table 1). Average damage to LA 1320 over these three seasons is 0.13%. Predicted damage to LA 1320 is $0.036 \times 8.5\% = 0.31\%$.

Fruit size and the weight of fruit per unit weight of vine cannot be manipulated much because of agronomic and marketing constraints. It may therefore not be possible to develop near immunity to *S. exigua* based on characteristics from LA 1320. Reduced larval preference for fruit can nevertheless result in a substantial reduction in damage by *S. exigua* that could be valuable as part of an integrated pest management program. Within-plant preference by insects for noneconomic tissues constitutes a form of tolerance (*sensu* Painter 1951). To be effective, this type of resistance requires that indirect effects of insect feeding on noneconomic tissues be minimal. Commercial tomatoes can tolerate 30% or greater defoliation before significant effects on yield can be measured (Wolk 1980, Welter & Steggal 1993), indicating that this crop is compatible with such a strategy.

The high TGA content of the fruit of LA 1310, LA 1320, and 'Tiny Tim' may contribute to reduced survival of *S. exigua* larvae on these fruit as compared with the fruit of susceptible 'VFN 7718'. The TGA content of the two *cer* lines was >13-fold that of 'VFN 7718'. TGA levels of 'Tiny Tim' are 2.5-fold that of 'VFN 7718'. TGA levels in *cer* and 'Tiny Tim' were much greater than the concentrations of α-tomatine toxic to *S. exigua* (Bloem et al. 1989). Equimolar quantities of phytosterols can alleviate tomatine toxicity (Bloem et al. 1989), but the fruit of all the lines tested had more tomatine than phytosterols on a molar basis.

Differences in fruit cuticle were unrelated to larval performance in our tests. NSL 27243 and LA 986 were specifically included in these experiments because they have unusual pericarp or cuticle characteristics that were considered likely to influence susceptibility. No evidence was found for this. However, the high larval mortality on 'Tiny Tim' may result from its slightly tougher cuticle (Tables 1 and 2) in combination with elevated α-tomatine concentrations as compared with 'VFN 7718'.

Juvik & Stevens (1982a) found no correlation between α-tomatine content and *S. exigua* survival on tomato fruits of three genotypes (one *cer,* or *pim,* and one *esc*) at five different ages, although α-tomatine concentrations in that study were similar to TGA concentrations we report here. Several factors may have caused this discrepancy. First, larvae in our tests were forced to feed exclusively on fruit, whereas in Juvik and Stevens' design larvae could feed on calyx and pedicel tissue as well as fruit. Second, the comparisons of Juvik & Stevens included five different fruit ages, introducing variation in other age-related factors. Third, our experiments were conducted with field-grown plants only, whereas those of Juvik & Stevens used glass house-grown potted plants. Finally, Phytosterol concentrations in the fruit tested by Juvik and Stevens may

have been higher than in our tests and modified the effects of tomatine on the larvae.

Juvik & Stevens (1982a) found a positive correlation between *S. exigua* survival and cuticle toughness on fruit from three genotypes at five different ages. The range of toughness values included in that study (150–650 g/mm^2), however, was much greater than in the present study (≈250–440 g/mm^2). Differences in cuticle toughness could not account for differences in genotype susceptibility within a single fruit age in the study by Juvik and Stevens, which is similar to our findings.

Our data indicate that α-tomatine content is a potential cause of antibiosis of the resistant fruit in this study. Additional experiments would be required to show that high tomatine levels actually cause this resistance. α-tomatine could also act as an antifeedant for *S. exigua* larvae and explain reduced feeding on fruit relative to foliage, which contains lower concentrations of this alkaloid than green mature fruits (Roddick 1974, Juvik & Stevens 1982b). Because larvae not only fed less on LA 1320 fruit but also were less likely to initiate feeding on this fruit, the observed preference must be caused by antifeedants on the surface of the fruit or to larvae learning to associate fruit surface characteristics of the resistant line with repellent or antifeedant properties of the pericarp. These possibilities will require additional study.

Elevated α-tomatine as a basis of fruit resistance would not necessarily pose a health risk to consumers. The concentration of this alkaloid drops markedly during the ripening process in cultivated and wild fruit of *L. esculentum* (Juvik & Stevens 1982a). A reduction in alkaloid content during ripening would not substantially reduce resistance in the field because the fruit of fresh-market tomatoes is normally picked just as the ripening process begins. Nevertheless, if the alkaloid is found to be necessary for the resistance, its concentration in ripe fruits of breeding lines must be monitored.

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